THE EFFECTS OF FIRE ON SPRUCE SEEDLING SURVIVAL AND TROPHIC INTERACTIONS IN THE HUDSON BAY LOWLANDS OF CHURCHILL, MANITOBA

MELISSA K. ANTONIADIS

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Abstract

This study examined how post-fire changes in abiotic and biotic conditions affect the performance and survival of spruce seedlings, and the abundance and diversity of insect and microbe communities in the subarctic of Churchill, Manitoba. This thesis also explored how varying colour of pan traps attract distinct groups of insect species, as pan trap colours mimic flower colours. In general, increased levels of all of the abiotic factors were found to positively influence the performance of spruce seedlings, except for soil organic matter. It was also found that the forest which was once dominated by white spruce shifted post-fire to mainly shrub land likely as a result of changes in abiotic conditions and plant interactions. The abundance of both arthropods and microbes was significantly greater in unburned areas compared to burned sites. Microbe concentrations were higher when measured on the ground compared to vegetative leaf surfaces, and yellow pan traps had the greatest arthropod capture rates.

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Thesis Introduction

In the Arctic, predicted changes as a result of climate change include warmer air and soil temperatures, more frequent forest fires, more rapid nutrient release from decomposing soil organic matter, and increased summer cloudiness as sea ice melts and allows greater evaporation from the ocean (Grau et al., 2012; Lloyd et al., 2010; Chapin et al., 1995; Shevtsova et al., 1997). In the subarctic region of Churchill, Manitoba specifically, data from the Churchill meteorological station showed an increase in mean temperature of 0.2°C per decade since 1901 and of 0.4°C per decade since 1976 (Monson, 2003). In Churchill, it is predicted that there will be longer warmer growing seasons, permafrost reduction, increased area burned due to changes in temperature and soil moisture and an overall increase in fire frequency (Monson, 2003). As the climate warms, the frequency and intensity of fires in the boreal forest is expected to increase, and has already been recorded in some parts of the region (Brown, 2010; Harden et al., 2000; Grau et al., 2012). In the entire North American boreal forest the average annual burned area has almost tripled, from an average of 1.11×10^6 ha during the 1960s to 3.04×10^6 ha during the 2000s, a likely result of climate change (Kasischke et al., 2006; Gillett et al., 2004; Kasischke & Turetsky, 2006). These environmental changes may potentially cause considerable direct and indirect effects on a multitude of ecosystem processes, including the advancement of the tree line northward (Shevtsova et al., 1997; Chapin et al., 1995). Tree line responses to climate change have particular significance in the Arctic where changes in the distribution of forested vegetation have potential feedbacks on regional and global climate (Lloyd et al., 2003; Lloyd et al., 2005; Iverson and Prasad, 1998).

Fire is a natural occurrence in northern regions, and can promote the establishment of trees and the subsequent advancement of tree lines by increasing nutrients, creating more favourable seedbeds, and also by reducing competition (Lloyd et al., 2003; Saxe et al., 2001; Brown, 2010; Kane et al., 1975; Harsch et al., 2009). The frequency of fires in the Boreal forest is variable, but historic fire-return intervals have been estimated to be around 80 to 120 years between fires, that is generally long enough for the re-establishment and recovery to maturity of trees before the subsequent fire (Brown, 2010). However, as the intensity and frequency of fires increases, the level of disturbance may increase beyond a threshold where trees are no longer capable of re-establishing; especially in northern areas where trees require long periods of time to reach maturity and reproduce successfully (Brown, 2010; Saxe et al., 2001). Growing conditions for trees in the forest-tundra ecotone tree line of the Boreal forest are not optimal, due to the underlying permafrost, which creates cold and wet soils with slow nutrient turnover rates (Brown, 2010; Grau et al., 2012). Thus, trees grow slowly and typically take several decades to reach reproductive maturity (Korner, 1998; Brown, 2010; Grau et al., 2012). Many tree species such as black spruce require long periods of time to reach reproductive maturity and to accumulate enough viable seed for self-replacement after fire (Monson, 2003; Saxe et al., 2001; Brown, 2010). Thus, understanding how Boreal forests will respond to fire is of significant importance.

Furthermore, disturbances such as fire can alter the balance between plants, and can also have cascading trophic effects on many levels of organisms in the ecosystem, including arthropods. Some plants, including spruce trees, may create a positive influence termed facilitation, in which at least one neighboring species benefits from the interaction through improved survival, growth, or fitness (Padilla and Pugnaire, 2006; Antonsson et al. 2009; Lortie

and Turkington, 2008). For instance, plants benefit arthropods by moderating temperature and moisture, and pollinators benefit by plants providing crucial floral resources (Coulson et al. 2003; Padilla and Pugnaire, 2006; Antonsson et al., 2009; Aredondo-Nunez et al., 2009; Molenda et al., 2012). However, it is unclear exactly how facilitative interactions will be altered in response to environmental change, and to what extent facilitation maintains biodiversity (Brooker et al., 2008). The *Stress Gradient Hypothesis* (SGH) is broadly supported and theorizes that the occurrence of positive interactions among plants increases with increasing stress in most environments (Antonsson et al., 2009; Liczner and Lortie, 2014).

However, the relationship between interactions and gradients of environmental severity is more complex than proposed in the original SGH (Brooker et al., 2008; Maestre and Cortina, 2004). For instance, one of the classic theories of plant community ecology to which the SGH is directly relevant is the hump-backed Intermediate Disturbance Hypothesis attributed to Connel (1978) (Brooker et al., 2008; Lortie and Turkington, 2008). Michalet et al. (2006) further developed this theory, suggesting that facilitation promotes diversity at medium to high environmental severity by expanding the range of stress-intolerant competitive species into harsh physical conditions, but that when environmental conditions become extremely severe the positive effects of the benefactors are weakened and diversity is reduced, indicating that biotic interactions shape both sides of the humped-back curve of diversity (Brooker et al., 2008). Thus, biotic interactions in ecosystems post-fire depend largely on the level of disturbance. Further, several studies have focused on plant-plant interactions, including facilitation, however effects of plants on higher trophic levels are rarely examined, and there are no studies to date in the Arctic (Liczner and Lortie, 2014; Reid, 2011). Also, current research on trophic facilitation is limited in

scope of taxinomical groups studied, typically focussing on aphids, beetles, and mites for example (Reid, 2011).

The objective of my research is to examine the response of white spruce seedlings to the potential impact of fire disturbance through changes in soil moisture, soil organic layer depth, and shading conditions, as well as plant interactions. Further, my research also seeks to examine the effects of fire on trophic interactions. Specifically, how fire and changes to spruce tree communities affect insect and microbe abundance and diversity. Finally, this thesis will also examine the related topic of how varying colour of pan traps attract distinct groups of insect species, as the pan trap colours mimic flower colours. These research questions collectively help us better understand the response of species and ecosystems to climate change and the relationship between biodiversity and ecosystem functions for northern ecosystems (Nyakata and McGeoch, 2008; Badano and Marquet, 2008; Shevtsova et al., 1997; Chapin et al., 1995; Eskelin, 2008).

Chapter 1. Spruce performance and survival after fire

The tree line is often referred to as an ecotone or area of transition between forest and tundra (Scott et al., 1984; Monson, 2003; Korner, 1998). As temperatures warm, tree lines are predicted to advance northward (Grau et al., 2012; Danby and Hik, 2001; Brown, 2010). Within this century, the *southern* borders of boreal forests are predicted to shift 500 to1000 km north, as natural competition and management convert up to 40 percent of present boreal forests into broad leaved temperate forests (Saxe et al., 2001). In the North, Arctic tundra is predicted to progressively, or by management, be invaded by boreal conifers (Emanuel et al., 1985; Prentice et al., 1991; Leemans, 1990; Woodward and Williams, 1987). However, findings from studies on the impacts of global environmental change on tree line dynamics have detected complex and often contradictory results as the advancement of trees into tundra in recent decades has been widespread but not universal (Harsch et al., 2009; Grau et al., 2012; Lloyd et al., 2003; Saxe et al., 2001; Hogg and Schwarz, 1997). Some studies on tree line response to climate change across the forest-tundra ecotone have found that tree lines have advanced while others have found an increase in stand density, or even a reduction or stagnancy in stand density, depending on species-specific traits and regional environmental conditions (Danby and Hik, 2001; Saxe et al., 2001; Hogg and Schwarz, 1997). Nevertheless, vegetation models generally predict a significant displacement of tundra by Boreal subarctic forest in response to future climate warming (Grau et al., 2011; Saxe et al., 2001).

Several factors have been found to control tree line advancement, including temperature, soil moisture, plant interactions, and fire, which is the dominant disturbance in Boreal forests (Grau et al., 2012; Brown, 2010; Danby and Hik, 2001). In the Boreal forest, crown fires that burn over large areas heterogeneously are prevalent, varying in severity, and creating changes in

vegetation and abiotic factors at the patch and landscape levels (Jayen et al., 2006; Johnstone and Chapin, 2006). Fire severity at ground level is often defined as the thickness of consumed organic matter (Jayen et al., 2006; van Wagner, 1983). The amount of soil organic matter consumed by a fire is a key influence on post-fire forest regeneration, including recruitment, establishment, survival, and performance (Johnstone and Chapin, 2006; Jayen et al., 2006). According to Johnstone and Chapin (2006), a multitude of studies have found a consistent steep decline in the establishment of conifers on residual organic soils of depths greater than 2.5 cm, while an increase in Boreal tree seedling recruitment, performance, and survival is observed when the burning of surface soil organic material exposed deeper mineral or organic soil layers (Jayen et al., 2006; Jarvis 1966; Chrosciewicz 1974; Clautice 1974; Zasada et al., 1983; Zasada 1985; Weber et al., 1987; Schimmel 1993; Charron and Greene 2002). However, other studies have found negative or neutral effects of burn severity on recruitment (Keays 1987; Schimmel 1993; Sirois 1993; Duchesne and Sirois, 1995). Overall, Johnstone and Chapin (2006) found that negative effects on seedling recruitment occurred beyond a certain threshold of burn severity, where deeply burned soils created moisture stress. Further, several studies have found soil moisture is positively correlated to spruce seedling performance, recruitment, and establishment after fire, whereas drought stress inhibits the performance of spruce seedlings (Kasischke et al., 2006; Wang et al., 2000; Bourgeau-Chavez et al., 2007; Kasischke et al., 2003; Danby and Hik, 2001). Therefore, spruce seedling performance may depend significantly on high levels of soil moisture availability independent of residual organic layer thickness, and moisture stress as a result of climate change and increasing fire severity/frequency may be an important limiting factor for tree line advancement.

Facilitation and competition are also important drivers of tree line dynamics, and these interactions are expected to shift as the environment changes; and as fires increase in frequency and severity (Grau et al., 2012; Maher et al., 2005). However, very little research has been conducted on tree line-shrub dynamics in subarctic ecosystems (Grau et al., 2012; Chrimes et al., 2005; Maher et al., 2005). Northern ecosystems consist of species-poor, slow-growing forests maintained in a delicate balance of plant interactions between the top canopy trees and understory shrubs and herbs (Mallik, 1995). The classic succession theory by Clements (1916) suggests that changes in species composition leads to a stable climax community that is similar to its pre-disturbance state; however in reality, some communities diverge from their pre-disturbance structure and follow an alternate successional path, as species interactions are strongly influenced by abiotic and biotic conditions (Collier and Mallik, 2010; Connell and Slayter, 1977; Tilman 1985; sensu Payette and Delwaide, 2003; Didham and Watts, 2005; Gleason, 1926). In stands dominated by spruce, little change in stand composition typically occurs after fire once the stands mature (Jayen et al., 2006 St-Pierre, Gagnon & Bellefleur, 1992; Lavoie & Sirois, 1998; Greene *et al.*, 1999; Greene & Johnson, 1999; Charron & Greene, 2002). However, removal of tree cover by fire may stimulate the growth of certain understory species and may negatively or positively affect tree seedling regeneration, depending on several factors including the severity of the disturbance, the abiotic conditions, and species-specific traits (Mallik, 1995). Thus, post-fire abiotic conditions are important for shaping plant interactions, and can result in inhibiting tree line advancement by competitive exclusion of certain conifer species.

The overarching hypothesis for this research is that fire negatively influences spruce seedling health and survival at the tree line in a subarctic ecosystem, limiting tree line

advancement northward. Spruce seedling performance after fire is directly driven by changes in fire severity, and resulting post-fire abiotic and biotic conditions. Hence, the following predictions were tested (1) Fire reshapes important biotic factors for spruce seedlings and their survival by reducing soil organic layer depth, soil moisture, and shading, and consequently post-fire abiotic conditions drive tree seedling survival and performance at the tree line, depending on the level of disturbance.

(2) Fire modifies abiotic factors and subsequently the composition of plant species in subarctic ecosystems by inhibiting or promoting the growth and survival of spruce seedlings through competition or facilitation.

Overall, these predictions address the mechanisms of spruce performance and plant interactions after fire.

Methods

Study site and plant species

Research was conducted over a six week period at the Twin Lakes study site near Churchill, Manitoba (Lat 58°46’06.28 N: Long 94°09’53.87 W) during the summer of 2013. The weather during the sampling period was unusually dry, as the mean total precipitation during the study period for July 2014 was 2.3 mm (standard deviation = 6.6), compared to the 30 year (1981 - 2010) precipitation normal of 59.8 mm (Appendix A, Environment Canada Historical Climate Data, 2015). Twin Lakes is a kame created during the retreat of the Laurentide ice sheet approximately 7600 years ago and contains two large kettle lakes which give the location its name. It stands approximately 30 m above the surrounding flat fens and bogs of the Hudson Bay Lowlands and is comprised largely of sandy till washed from the receding glacier. It supports a

very distinct (for the region) Boreal community of open canopy spruce-lichen woodland and was designated as a site of special ecological significance by the International Biological Program (Johnson, 1984). The dominant plant species at this site include *Picea mariana* (black spruce), *Picea glauca* (white spruce), *Salix ssp* (willow), and *Betula glandulosa* (dwarf birch) shrubs. A ground based view of the burned area is shown and an aerial image of the site was used to select study sites (Figures 1.1 and 1.2). The study site was selected because there were two overlapping forest fires at Twin Lakes in 1990 and 1997 (Figure 1.2 outline extents). Four transects were set up containing 10x2m quadrats at 10m intervals, delineated by rope and flags. Transect 1 (1,460 m) and 2 (1,400 m) were situated in the eastern portion of the burn, running along the side of a trail from the north edge of the burn to the south edge of the burn, and into unburned black spruce forest at the southern edge. Transect 1 ran along the east side of a trail and Transect 2 ran along the west side of the trail. Transect 3 (8,000 m) was situated in the western part of the burn, running north-south parallel to another trail. Transect 4 (8,400 m) ran west-east, intersecting with all other transects (Figure 1.2).

Within each quadrat, every spruce seedling was considered a plot, and in quadrats containing no spruce seedlings, the top left (north-west) corner, middle, and bottom right (south-east) corners on a diagonal across the quadrats were considered plots, and each plot was tagged with flag tape and labelled alphabetically and according to quadrat number (i.e. 1a).

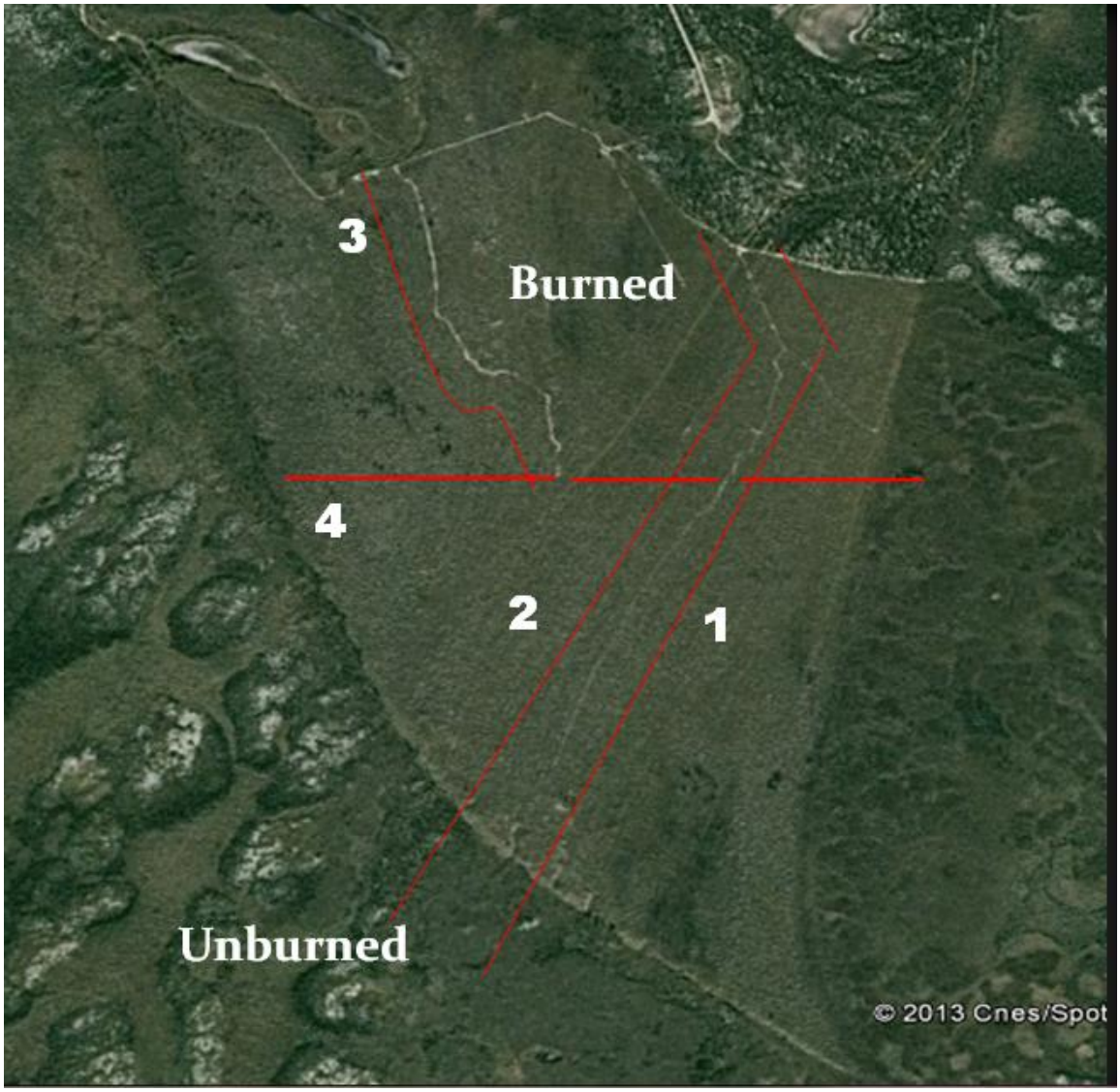

Figure 1.1. Map of study site and transects at Twin Lakes.

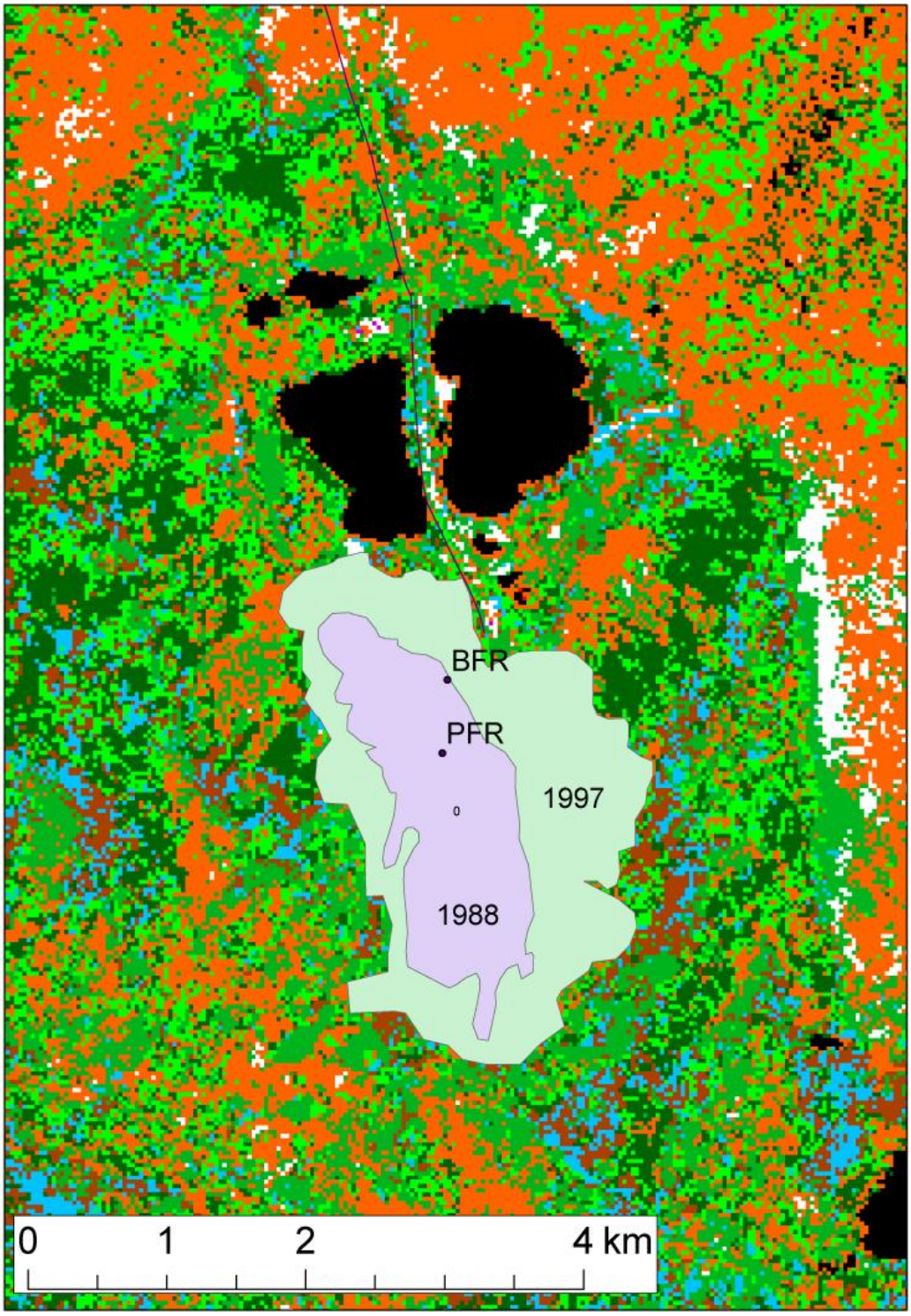

Figure 1.2. Aerial image of Twin Lakes sampling site showing the two overlapping fires in 1990 and 1997.

Abiotic & Biotic Factors

At each plot latitude and longitude were recorded using a GPS, along with estimated plant cover in tenths, soil organic layer thickness using a soil auger (mm), average surface soil moisture (top 6 cm) with a DeltaT Theta probe, and paired readings of sunlight (PPFD) using a LICOR LI190 quantum sensor at breast height and ground level. To control for temporal variability, soil moisture and sunlight were recorded within a one day period on each transect.

For quadrats with spruce seedlings, quantum yield was also measured using a hand-held chlorophyll fluorometer (FP100max, Photon Systems Inc.) on a single spruce needle near the top of the seedling. Stem diameter (mm) was also determined with a digital caliper (±0.1 mm) approximately 10cm below the top of each spruce seedling. Seedling height and distance to the nearest neighbour was measured (cm) using a measuring tape. The number of whorls were also recorded as an age estimate (Makinen, 1999), and health and needle density were estimated on a likert scale from 1 to 3, with 1 being unhealthy/low needle density and 3 being very healthy/high needle density (Matell and Jacoby, 1971).

Statistical analyses

To reduce the number of factors, a principal component analysis (PCA) was conducted using SPSS 22 (IBM SPSS 22, 2013; Townend, 2002). Two components, age and height, were responsible for 88% of the correlated variation and subsequently used in all additional analyses (Table 1.5). To assess whether there is an abiotic effect on tree age, a generalized linear model (GLM) with soil moisture, soil organic matter depth, and sunlight percent transmission as factors, burned/unburned plots as covariates, was applied to the spruce performance measures recorded. Mean data per quadrat was used for the GLM with mean tree density as a response

variable, and raw data per spruce tree/plot was used for the other GLMs. To test for significant differences in abiotic variables between burned and unburned plots a Multivariate ANOVA was conducted using SPSS 22 (IBM SPSS 22, 2013). An ANOVA was also performed to assess whether there is a difference in spruce seedling age and height between organic matter depths grouped into low (<2.5 cm) and high (>2.5 cm) using SPSS 22 (IBM SPSS 22, 2013). For all analyses, significant effects were considered at the alpha levels of $p<0.05$ and were done using SPSS 22 (IBM SPSS 22, 2013)

Results

Spruce trees were significantly older in plots with higher soil moisture levels (Table 1.1, $p = 0.026$, $df = 1$). There were no other significant abiotic factors or interaction effects on tree age (Table 1.1) At burned sites, soil moisture and sunlight transmission were positively related to tree height but soil organic matter depth was unrelated (Table 1.1, $p = < 0.001$, $df = 1$ for both). Burned plots with increased sunlight transmission also had significantly higher mean tree density compared to unburned plots (Table 1.1, $p = 0.003$, $p = 0.011$ respectively, $df = 1$). Significant differences were found between burned and unburned plots for soil moisture, soil organic matter depth, and sunlight (Figure 1.4, Table 1.2, $p = < 0.001$, $df = 1$).

Discussion

The general hypothesis that fire is the dominant factor in controlling spruce seedlings in a Boreal system at the tree line was supported. In burned plots with high levels of sunlight transmission, mean tree density was greater compared to unburned plots. Also, in burned plots with increased sunlight and soil moisture spruce seedlings were taller compared to unburned plots. Spruce seedlings were also found to be older in all plots with increased soil moisture

levels. Thus, this study suggests that moisture and sunlight are important factors for spruce seedlings performance and survival in the subarctic.

This study provides useful ground truth data on soil moisture, soil organic matter depth, and sunlight typically used in Global Circulation Models (GCM) to predict how the tree line will be altered in response to climate change (IPCC, 2012; Fyllas and Troumbis, 2009; Calef et al., 2005; Danby and Hik, 2001; Heikkinen et al., 2006; Prentice et al., 1991. Findings from the current study suggest that as the climate warms post-fire abiotic conditions may become too stressful for spruce seedlings to cope, and consequently conifers such as spruce may be replaced by deciduous species, potentially altering the structure and composition of the tree line (Danby and Hik, 2001; Brown, 2010; Laliberte and Payette, 2008). The cover data from this study at Twin Lakes shows that willow and birch shrubs are the dominant vegetation in a forest that was originally black spruce and white spruce. Further, findings from this study also suggest that a reduction in shading increases spruce seedling density and tree height, especially in burned plots, demonstrating the importance of sunlight after fire, and the negative competitive interaction effects shrubs can create for spruce seedling, establishment, survival, and performance. In the subarctic, competition for light is thought to be important, as many macro lichens often operate at light regimes below their photosynthetic light saturation point (Cornellisen et al., 2001). Increased shading in response to increased plant growth as a result of regional warming at high latitudes would thus be expected to inhibit the performance of certain neighbouring species, and may lead to competition for light (Cornellisen et al., 2001). Very little research has been conducted on tree line-shrub dynamics in arctic ecosystems, and most findings from the existing research (Grau et al., 2012; Chrimes et al., 2005; Maher et al., 2005) show that shrubs have been found to facilitate tree seedlings after fire and/or in harsh environmental conditions, which

contradicts findings from this study, where shrubs were found to inhibit the establishment and performance of spruce seedlings as a result of changes in post-fire abiotic conditions, and competition for resources. This research demonstrates the importance of understanding how spruce tree communities will respond to disturbance, and has significant implications for tree planting and forest management after fires, as certain species, such as spruce may be incapable of post-fire replacement in northern regions as fires become more frequent and severe.

Also, the distribution of vegetation types is strongly determined by temperature in the high latitudes, and as this study suggests moisture is also a key factor – as temperatures rise moisture stress is also expected to increase, potentially limiting tree line advancement North (Prentice et al., 1991; Lloyd et al., 2007; Danby and Hik, 2001; Iverson and Prasad, 1998). In a normal precipitation year it likely would have been difficult to find significant differences in moisture between sites, as soil moisture is extremely variable over time and space, making it difficult to record reliable soil moisture readings. Soil moisture data from the current study was collected during an unusually dry summer, which provided the ability to identify a significant moisture dependence. Thus, this study was unique, as the unusual weather conditions allowed for the opportunity to measure soil moisture reliably in a short time frame over great distances. Findings from this study have important implications for tree line forests, as it is likely the extreme years which have the greatest impact on spruce tree growth and survival. Findings from this study provide useful insights into spruce seedling responses to stressful moisture conditions at the tree line, as moisture stress is expected to increase as temperatures rise and as fires become more frequent and severe. Tree line forests are likely to be sensitive to direct climate effects because these forests are located in areas of the extreme conditions of species tolerance limits, and the current study shows that as fires become more frequent and severe spruce trees may be

replaced by other plant species, as it is possible that they are unable to cope with stressful abiotic conditions (Brown, 2010; Saxe et al., 2001; Danby and Hik, 2001; Iverson and Prasad, 1998; Korner, 1998). Although trees have responded to climate warming in the past to temperatures higher than current temperatures, the rate of change predicted in the 21st century is predicted to be unprecedented (Saxe et al., 2001; Prentice et al., 1991; Lloyd et al., 2010; Walther et al., 2007). Predicted emissions of greenhouse gases in this century could cause a 3° C to 6° C increase in mean land surface temperature at high and temperate latitudes and over the last 30 years annual surface temperatures have increased by about 5° C in Canadian boreal regions (Harden et al., 2000; Saxe et al., 2001).

Furthermore, several studies have found that organic soils of depths greater than 2.5 cm negatively affect boreal tree seedling recruitment, performance, and survival (Jayen et al., 2006; Jarvis 1966; Chrosciewicz 1974; Clautice 1974; Zasada et al., 1983; Zasada 1985; Weber et al., 1987; Schimmel 1993; Charron and Greene 2002), while some studies have found negative or neutral effects of soil organic layer depths of less than 2.5 cm after fire (Keays 1987; Schimmel 1993; Sirois 1993; Duchesne and Sirois, 1995). Although soil organic matter depth was significantly greater in unburned sites compared to burned sites, findings from this study show that there were no significant effects for soil organic matter depth on any of the spruce performance measures, suggesting that soil moisture and sunlight may be more important factors for studying spruce seedling performance and tree line dynamics in northern regions. These results were surprising, however as it was an unusually dry period it is possible that soil organic matter was independent of soil moisture, because when moisture levels are extremely low soil type and characteristics such as water retention or porosity would not play an important role for spruce seedlings. Findings from this study have important implications for tree line forests,

demonstrating that spruce seedling performance may depend significantly on high levels of soil moisture availability independent of residual organic layer thickness, and moisture stress as a result of climate change and increasing fire severity/frequency may be an important limiting factor for tree line advancement. Thus, as 10 times more land area burned than in any previous decade on record in the 1980s (Harden et al., 2000) and Flannigan and Van Wagner (1991) predicted a possible 46 percent increase in burn area for the Canadian boreal forest under a doubling of CO_2 climate scenario, it is important to understand and monitor how plants respond to fire, and the mechanisms responsible for tree seedling establishment, and survival post-fire.

Tables

Table 1.1. Summary table of GLMs testing the effect of soil moisture, soil organic matter depth, and sunlight percent transmission, and the interaction of burned plots compared to unburned plots on spruce seedling age, height, and mean tree density per quadrat. Soil moisture (%), soil organic matter depth (cm), and sunlight percent transmission were modeled as factors, and burned/unburned plots were modeled as covariates. Age is the number of whorls. Statistical significance at $p < 0.05$ is indicated with bold font.

		Age		**Height (cm)**		**Mean tree density**	
Factor	**df**	x2	**p-value**	x2	**p-value**	x2	**p-value**
Soil moisture	1	4.93	**0.026**	76.47	< **0.0001**	0.07	0.798
Soil om depth	1	0.24	0.623	8.217	**0.004**	1.74	0.187
Sunlight	1	0.01	0.921	12.60	< **0.0001**	8.59	**0.003**
Burned/unburned* soil moisture	1	0.00	0.962	19.11	< **0.0001**	0.04	0.839
Burned/unburned* soil om depth	1	0.27	0.607	2.04	0.153	2.80	0.094
Burned/unburned* sunlight	1	2.43	0.119	27.82	< **0.0001**	6.39	**0.011**
Shade cover	1	N/A	N/A	N/A	N/A	0.45	0.504

Table 1.2. Multivariate ANOVA comparing soil moisture %, soil organic matter depth (cm), and sunlight % transmission between burned and unburned plots, all transects combined. Statistical significance at $p < 0.05$ is indicated with bold font.

Multivariate Tests

Effect		Value	F	Hypothesis df	Error df	Sig.
Intercept	Pillai's Trace	.806	621.403[b]	3.000	448.000	.000
	Wilks' Lambda	.194	621.403[b]	3.000	448.000	.000
	Hotelling's Trace	4.161	621.403[b]	3.000	448.000	.000
	Roy's Largest Root	4.161	621.403[b]	3.000	448.000	.000
burn	Pillai's Trace	.122	20.835[b]	3.000	448.000	.000
	Wilks' Lambda	.878	20.835[b]	3.000	448.000	.000
	Hotelling's Trace	.140	20.835[b]	3.000	448.000	.000
	Roy's Largest Root	.140	20.835[b]	3.000	448.000	.000

Tests of Between-Subjects Effects

Source	Dependent Variable	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	OM depth (cm)	239.894[a]	1	239.894	34.520	.000
	Soil moisture (%)	736.521[b]	1	736.521	23.399	.000
	Sunlight (%) transmission	.621[c]	1	.621	10.326	.001
Intercept	OM depth (cm)	2934.329	1	2934.329	422.247	.000
	Soil moisture (%)	22808.460	1	22808.460	724.601	.000
	Sunlight (%) transmission	19.388	1	19.388	322.162	.000
burn	OM depth (cm)	239.894	1	239.894	34.520	.000
	Soil moisture (%)	736.521	1	736.521	23.399	.000
	Sunlight (%) transmission	.621	1	.621	10.326	.001
Error	OM depth (cm)	3127.194	450	6.949		
	Soil moisture (%)	14164.766	450	31.477		
	Sunlight (%) transmission	27.081	450	.060		
Total	OM depth (cm)	13783.472	452			
	Soil moisture (%)	118778.820	452			
	Sunlight (%) transmission	199.679	452			
Corrected Total	OM depth (cm)	3367.088	451			
	Soil moisture (%)	14901.287	451			
	Sunlight (%) transmission	27.703	451			

a. R Squared = .071 (Adjusted R Squared = .069)
b. R Squared = .049 (Adjusted R Squared = .047)
c. R Squared = .022 (Adjusted R Squared = .020)

Figures

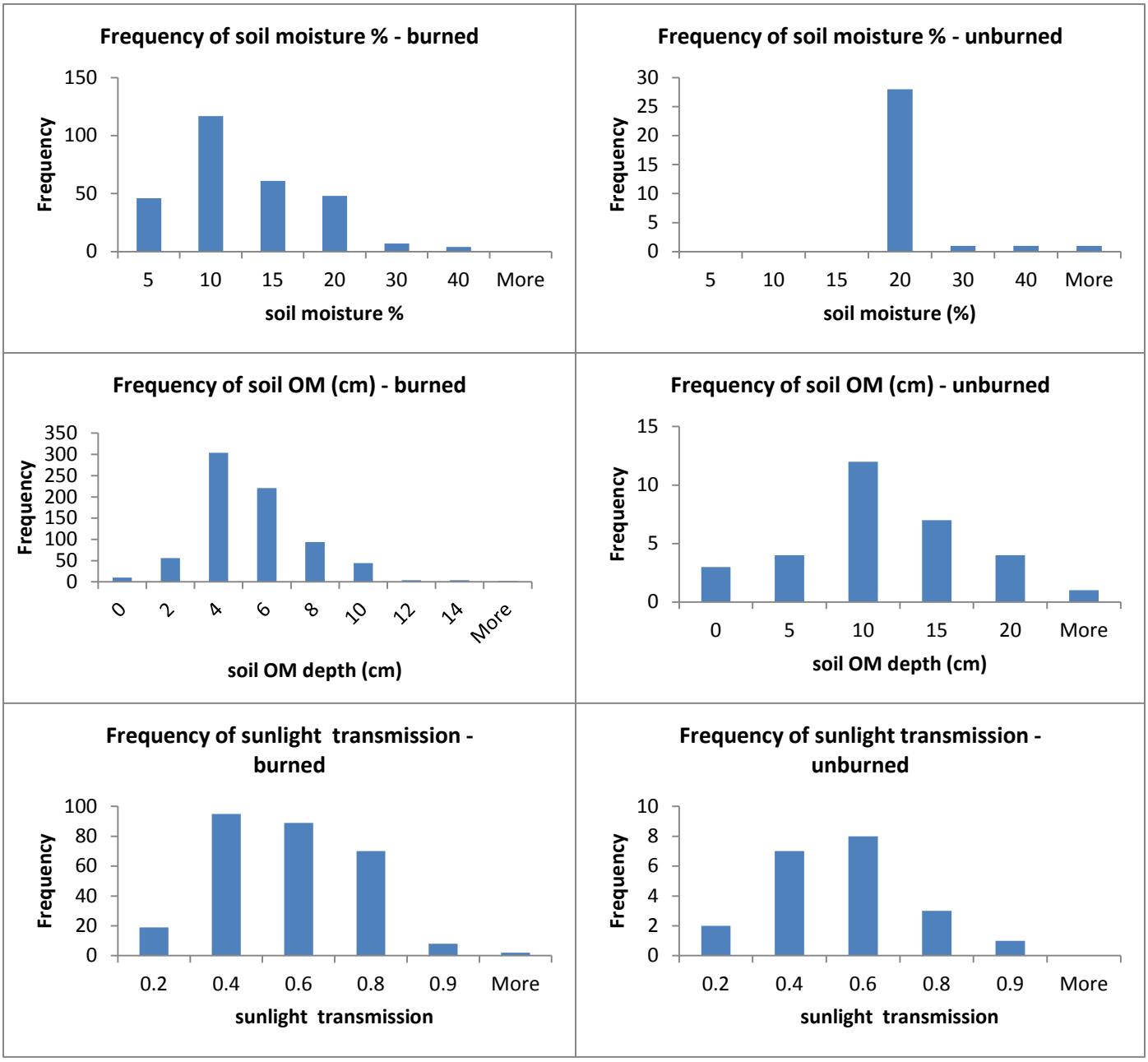

Figure 1.3. Frequency distribution of soil moisture (%), soil organic matter depth (cm), and sunlight transmission in burned plots and unburned plots, using the raw data from all transects combined.

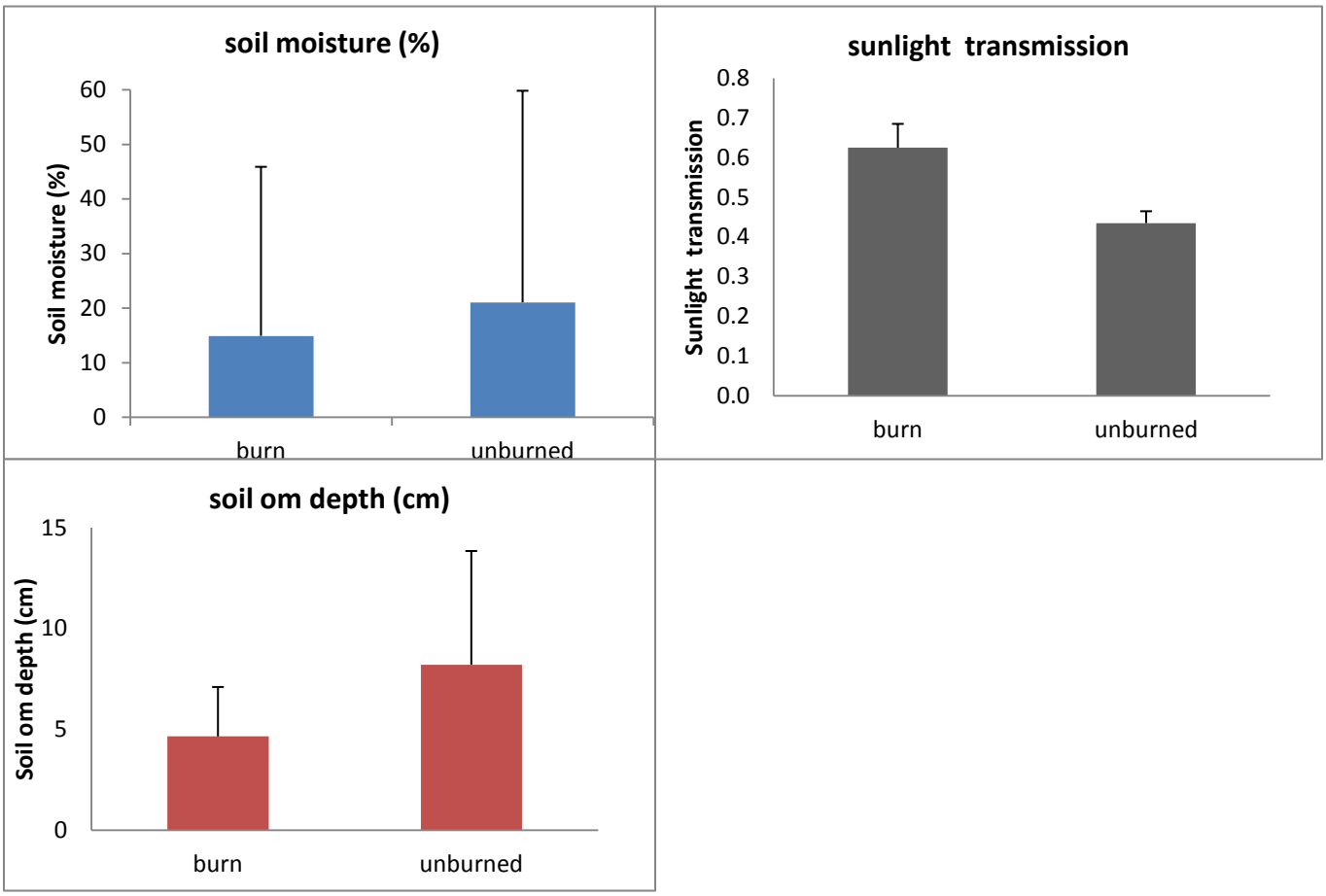

Figure 1.4. Comparison of average volumetric soil moisture % (A), soil organic matter depth (cm) (B), and sunlight transmission (C) between burned and unburned plots using the raw data.

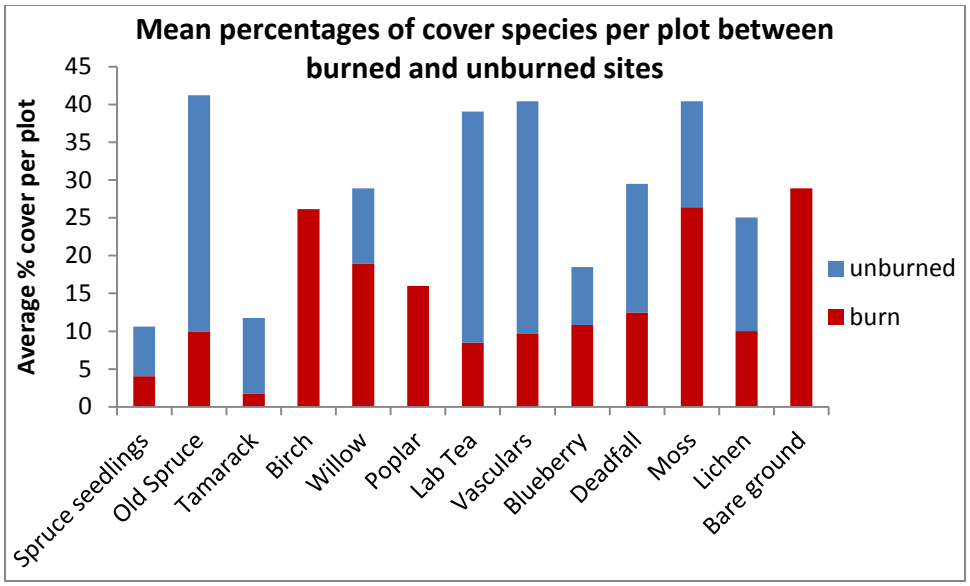

Figure 1.5. Average % cover of species per plot for burned and unburned sites, all transects combined. The dominant plant species are listed, and all other vascular plant species were grouped into "Vasculars."

Chapter 2

Effects of fire on arthropods & microbes in a Boreal ecosystem.

Plants influence their neighbours and other trophic levels in many ways thereby generating a broad range of negative or positive outcomes. Competing for light, nutrients, space, and water while at the same time protecting one another from the impacts of herbivores, potential competitors, or extreme climates (Padilla and Pugnaire, 2006; Reid, 2011; Brooker et al., 2008; Acuna-Rodrigues et al., 2006; Antonsson et al., 2009; Molenda et al., 2012) can lead to very different assemblages of species, and both positive and negative effects can of course co-occur (Wipf et al., 2006; Eskelin, 2008). The nurse effect is a particular kind of positive interaction wherein one species, the nurse - often a dominant plant species, provides microclimatic conditions that enhance the establishment, survival, and growth for the beneficiary or associated species, and the positive effects of growing close together outweigh the negative, competitive effects (Acuna-Rodrigues et al., 2006; Antonsson et al., 2009). The nurse effect of plants has been shown to increase species diversity of plants (Brooker et al., 2008; Badano and Marquet, 2008; Reid, 2011; Molenda et al., 2012), arthropods (Coulson et al., 2003; Reid, 2011; Molenda et al., 2012; Corbet, 1995), by acting as drivers of succession. Collectively however, the loss of these dominant plants on the facilitative effects for the community is rarely examined (but see – Arredondo-Nunez et al., 2009; Badano and Cavieres, 2006).

Plant facilitation is an integral component of community assembly and is an important consideration in light of global change. Arctic habitats are predicted to be among the most sensitive to global warming and increased fire disturbance (Antonsson et al., 2009; Badano and Marquet, 2008; Reid, 2011; Brooker et al., 2008; Shevstova et al., 1997; Chapin et al., 1995; Eskelin, 2008; Sonesson et al. 2002, Wipf, 2006; Pouliot et al., 2011; Molenda et al., 2012).

More extreme environments are also very likely to be shaped by strong facilitation between plants (Sonesson et al., 2002; Eskelin, 2008; Badano and Marquet, 2008; Arredondo-Nunez et al., 2009). However, it is unclear exactly how facilitative interactions will be altered in response to environmental change in these ecosystems and to what extent facilitation maintains biodiversity (Brooker et al., 2008) particularly with a changing climate differentially impacting dominants from other plant species. Consequently, disturbances such as fire in the Arctic can alter the outcome of the interactions between plants (Acuna-Rodrigues et al., 2006; Chapin et al., 1995; Padilla and Pugnaire, 2006), and it is thus reasonable to propose that these new outcomes have cascading trophic effects (Christiansen and Lavigne, 2010; Clausen, 1986; Koponen, 1995) on many levels of organisms in the ecosystem including arthropods. Several studies have found that post-fire microbial communities are often less diverse and their composition can be influenced by factors such as changes in soil moisture availability, soil pH, and nutrients (Weber et al., 2014; Acea and Carballas, 1996; Dumontet et al., 1996; Prieto-Fernandez et al., 1998; Certini, 2005; Smithwick et al., 2005; Yeager et al., 2005; Jackson et al., 2006; Mabuhay et al., 2006; Hamman et al., 2007; Dangi et al., 2010; Barcenas-Moreno et al., 2011; Sun et al., 2011; Docherty et al., 2012; Ginzburg and Steinberger, 2012; Goberna et al., 2012). However, fewer studies have examined the impact of fire on arthropods (Taylor and Catling, 2011; Moretti et al., 2002; Richert and Reeder, 1972) Also, there are no studies to date in the Arctic on spruce tree or willow shrub facilitation of arthropods or microbes. Thus given the fact that Arctic systems are predicted to experience extremes in climate including altered fire regimes, exploring the effect of changes in dominant plants is an important research topic.

The hypothesis for this research is that fire negatively affects arthropod and microbe abundance at the treeline in a subarctic ecosystem by removing spruce and willow plants. The

following predictions were tested. 1. Arthropod and microbe densities and diversities are higher at sites with willow and spruce present, i.e. unburned vs burned sites. 2. Abiotic drivers such as changes in soil moisture, soil organic matter depth, and sunlight as a result of fire reduce arthropod and microbe abundances and diversities. 3. Total number of plant species is also reduced by fire and thus lower plant species diversity correlates with lower insect and microbe abundance. Arthropod colour preference for pan traps as a sampling method to capture insects was also tested as research in the Arctic is limited. The main goal of this pilot study is to therefore add to the baseline understanding of plant-insect/microbe associations in the subarctic and explore the importance of a changing fire regime due to climate change and more generally examine whether these techniques are viable in this ecosystem.

Methods

Research was conducted at the Twin Lakes study site near Churchill, Manitoba (Lat 58°46’06.28 N: Long 94°09’53.87 W) during the summer of 2013. The weather during the sampling period was unusually dry, as the mean total precipitation during the study period for July 2014 was 2.3 mm (standard deviation = 6.6), compared to the 30 year (1981 - 2010) precipitation normal of 59.8 mm (Appendix B, Environment Canada Historical Climate Data, 2015). Twin Lakes is a kame created during the retreat of the Laurentide ice sheet approximately 7600 years ago and contains two large kettle lakes which give the location its name. It stands approximately 30 m above the surrounding flat fens and bogs of the Hudson Bay Lowlands and is comprised largely of sandy till washed from the receding glacier. It supports a very distinct (for the region) Boreal community of open canopy spruce-lichen woodland and was designated as a site of special ecological significance by the International Biological Program (Johnson, 1984). The dominant plant species at this site include *Picea mariana* (black spruce),

Picea glauca (white spruce), *Salix ssp* (willow), and *Betula glandulosa* (dwarf birch) shrubs. A ground based view of the burned area is shown and an aerial image of the site was used to select study sites (Figures 1.1 and 1.2). The study site was selected because there were two overlapping forest fires at Twin Lakes in 1990 and 1997 (Figure 1.2 outline extents). Four transects were set up containing 10x2m quadrats at 10m intervals, delineated by rope and flags. Transect 1 (1,460 m) and 2 (1,400 m) were situated in the eastern portion of the burn, running along the side of a trail from the north edge of the burn to the south edge of the burn, and into unburned black spruce forest at the southern edge. Transect 1 ran along the east side of a trail and Transect 2 ran along the west side of the trail. Transect 3 (8,000 m) was situated in the western part of the burn, running north-south parallel to another trail. Transect 4 (8,400 m) ran west-east, intersecting with all other transects (Figure 1.2).

Insect and microbe sampling designs

For insect diversity and abundance, a total of 50 plots in the unburned forest and 50 plots in the burnt, open (but previously forested) sites were used (N=100). In each burned and unburned site 25 spruce trees and 25 willow shrubs were selected for sampling and tagged. At each of the marked plants, microbes (cyanobacteria, green algae, and diatoms) were also measured on July 25th, 2013 using a Bentho-torch (Kahlert and McKie, 2014). The Bentho-torch was used to take chlorophyll fluorescence readings from a 2.5 cm diameter field of view on a lower branch of each spruce and willow and directly below each spruce and willow on the bare soil. Extraneous light from below was excluded by placing branches on a black notebook and from above by placing a fabric shroud over the measurement apparatus. To capture insects, pan traps were spray painted yellow, blue, or white using fluorescent paint, and approximately 2 cups of Dawn dish soap was diluted in approximately 1 gallon of water (Nserc-Canpolin protocol -

Canadian Pollination Initiative, 2015). On July 24th, 2013 at 11:30am, one yellow, one white, and one blue pan trap were placed directly beneath each spruce or willow tree. Pan traps were filled halfway to the top with the water and soap mixed. The following day between 11:30am and 1pm, all pan traps were collected and insects removed. Although only one replicate was performed, this pilot study provides a snapshot of insect dynamics as insects were collected during the relatively short, peak insect biomass season for Churchill (Figure 2.6) during the month of July (Zhou et al., 2009; Zhou et al., 2010; Senner, 2013; McClure, 1943). After all of the insects were collected, the vials were filled with pure ethanol and individual insects were identified to functional groups at a later date.

Statistical analyses

For the arthropods the number of factors was reduced using a principle component analysis (PCA) for insect groups by pan trap colour as factors. The results from the PCA indicated that the blue pan trap colour was not a significant factor and was thus removed from further analyses. To assess whether there is a burned/unburned site, vegetation type (spruce/willow), or pan trap colour (yellow/white) effect on arthropod abundance, a generalized linear model (GLM) was used to test for effects on the functional groupings of insects including crawlers, winged, pollinators, and also total abundance. To test whether the community composition of the insects differed between burned/unburned sites an ordination analyses, NMDS, and MRPP was conducted. A generalized linear model (GLM) was used to test for an effect of burn history and tree species presence on the relative concentrations of green algae, cyanobacteria, diatoms, and total microbial concentration. The GLMs and PCA were done in SPSS 22 (IBM SPSS, 2013) and the NMDS was done in PC-ORD 5 (MJM Software Design PC-ORD, 1999).

Results

Insect abundance for all functional groups was significantly higher in unburned sites compared to burned sites (Figure 2.3, Table 2.1, p = <0.0001, <0.0001, 0.007, p = 0.011). Overall, winged arthropods were more prevalent than crawling insects and very few pollinators such as bees were captured (Figure 2.1). Yellow pan traps had the greatest affect on arthropod capture rates for all functional groups and total insect abundance (Figure 2.2, Table 2.1, p = <0.0001, p = <0.0001, p = 0.054, p = <0.0001). Community composition was significantly different between burned and unburned sites (Figure 2.3, Table 2.2, p = <0.001, df = 1). Also, significant effects were found for pan trap placement below spruce for winged insects only (Table 2.3, p = 0.002, df = 1).

There was a significant interaction effect of unburned plots with vegetation for cyanobacteria, diatom, and total concentration of microbes (Table 2.3, p = < 0.0001 except for vegetation type and diatoms p = 0.006; and vegetation type and total concentration p = 0.002, df = 1). Green algae concentrations were greater at unburned sites on both spruce and willows (Figure 2.4, Table 2.3, p = 0.006, df = 1).

Discussion

Overall, the hypothesis that fire reduces insect and microbial abundances in subarctic systems was supported even with the presence of the dominant plant species at those sites. Insect and microbial abundance was significantly greater in unburned sites compared to burned sites. Several studies have found that in ecosystems where fires are frequent and of low to medium intensity fire can increase arthropod abundance and diversity by changing habitat structure and opening new habitat niches (Moretti et al., 2002; York, 2000; Siemann, Haarstad & Tilman

1997, in oak-savannah; Riechert & Reeder 1972). However, in the subarctic Boreal forest, where it is predicted that fires will become more frequent and severe arthropod communities may not be able to adapt to these changes. In such ecosystems with very long fire-turnover intervals (20 years or more) the species richness and abundance of arthropod communities have been observed to decrease over the long-term after intensive fires, which is consistent with findings from this study where insect abundance was significantly lower in burned sites compared to unburned sites (Moretti et al., 2002; Huhta 1971; Koponen 1995; Hauge & Kvamme 1983). Although only one replicate of insect sampling was performed, insect collection took place during the peak insect biomass season for Churchill in July and a large sample size was used in order to provide an initial snapshot of insect dynamics (Zhou et al., 2009; Zhou et al., 2010; Senner, 2013; McClure, 1943).

Results from this study also support the hypothesis that abiotic drivers such as changes in soil moisture, soil organic matter depth, and sunlight as a result of fire can reduce arthropod abundance and diversity. Arthropod community composition was significantly different in burned sites compared to unburned sites, and in burned sites where insect abundance was decreased there were also low levels of soil moisture, soil organic matter, and shading compared to unburned sites. The pattern of soil insulation or shading has been found to be a key factor for controlling ant and spider abundance, as it has a direct effect on the temperature of the nest-site and an indirect effect on food supply from vegetation (York, 2000; Moretti et al., 2002). Thus, decreasing levels of shading and changes in surface and nest temperatures with decreasing vegetation cover over time may reduce arthropod species richness (Goldstein 1975; Greenslade & Mott 1979) and alter community composition as the environmental conditions become suboptimal for certain species (Welch 1978; Elmes & Wardlaw 1982). Terrestrial invertebrate

populations have also been shown to be strongly influenced by the moisture and organic matter content of the litter (Spain & Hutson 1983). Therefore, as climate change is expected to be most apparent in arctic ecosystems this study has important implications for the arthropod community, especially as the study was conducted during a drought year, providing the opportunity to study arthropod community composition during extreme conditions.

Furthermore, the removal of vegetation cover by fire has been found to play a key role in reducing arthropod abundance, mainly a result of altered habitat conditions, specifically litter biomass, vegetation structure and patterns of ground insulation (York, 2000). This study also supports the hypothesis that dominant plant species such as spruce and willow in Boreal systems facilitate arthropod and microbial communities. Insect abundance was significantly lower in burned sites where mean spruce tree density was decreased and spruce trees were younger and shorter compared to unburned sites, and the community composition of insects was significantly different between burned and unburned sites. Also, although only two vegetative species were tested, winged insects showed a strong preference for spruce, suggesting that spruce may be important for the facilitation of winged insects, especially after fire. The presence of ecosystem engineers in natural communities such as spruce and willow inevitably increases species richness, because the creation of engineered patches typically increases habitat diversity in the landscape and, hence, the number of available niches for other species, and thus the removal of plants by fire can lead to a reduction in the abundance and diversity of other communities of species (Badano and Cavieres, 2006; Nunez et al., 1999; Reid, 2011; Padilla and Pugnaire, 2006).

Therefore, this study has important implications for forest conservation and management efforts, especially after fire in the subarctic, as the results demonstrate that the removal of

foundation plant species can have devastating effects on arthropod communities. There is very little research to date on the effects of fire on invertebrate communities in the subarctic, and all of these studies focus on patterns of invasive or parasitic insects after fire. This is concerning given that invertebrates comprise the majority of the biodiversity in these subarctic ecosystems and play an essential role in forest ecological processes including nutrient cycling, decomposition, and seed dispersal (Christiansen and Lavigne, 2010; York, 2000). Particular groups of arthropods react sensitively to ecosystem disturbances such as fires including spiders and ants, thus these groups can be used as ecological indicators (Moretti et al., 2002; Clausen 1986; Bauchhness 1990; Wise 1993; Canard, Marc & Ysnel 1998).

Overall, the hypothesis that microbe concentrations would be greatest in unburned sites compared to burned sites and for measurements taken on the ground compared to on vegetative leaf surfaces was supported. All microbe types, including cyanobacteria, green algae, diatoms, and total concentration microbial concentrations were highest in unburned sites, and green algae was the only microbe type that was not significantly affected by vegetation type and the interaction of vegetation type and burned vs unburned sites. These results support research from Weber et al. (2014) who found that microbial richness was lower in highly burned soils compared to unburned soils in mixed conifer forests. Further, several studies have found that post-fire microbial communities are often less diverse and their composition may be influenced by factors such as changes in soil moisture availability, soil pH and nutrients, supporting the hypothesis that abiotic drivers such as changes in soil moisture, soil organic matter depth, and sunlight as a result of fire reduce microbial abundance and diversity. (Weber et al., 2014; Acea and Carballas, 1996; Dumontet et al., 1996; Prieto-Fernandez et al., 1998; Certini, 2005; Smithwick et al., 2005; Yeager et al., 2005; Jackson et al., 2006; Mabuhay et al., 2006; Hamman

et al., 2007; Dangi et al., 2010; Barcenas-Moreno et al., 2011; Sun et al., 2011; Docherty et al., 2012; Ginzburg and Steinberger, 2012; Goberna et al., 2012). Also, in support of these findings, Weber et al. (2014) found that soil bacterial composition shifted as a group in response to dramatic decreased soil moisture and organic matter post-fire, suggesting that changes in the abiotic conditions measured in this study can influence microbial composition post-fire and decrease the diversity of microbial communities as a whole. Further, changes in vegetation structure and composition post-fire can alter microbial community richness (Treves et al., 2003), as microbe abundance and diversity was significantly lower in burned sites where mean spruce tree density was lower, and spruce trees were younger and shorter compared to unburned sites.

However, to date these studies have typically utilized coarse-resolution DNA fingerprinting methods and phospholipid fatty acid profiles – the Bentho-torch method used in this study is an innovative method, and there is no existing research to date using this technology to study microbe concentrations in three algal classes on northern ecosystems post-fire. Further, plants provide an extremely diverse habitat for microorganisms, and each zone of a plant has its own group of microorganisms with varied relationships (Andrews et al., 2000). Through recent technological breakthroughs, such as the Bentho-torch used in this study, the scientific community is gaining a better perspective of the nature of these relationships, yet still relatively little is known about the role of microbial associations with plants (Andrews et al., 2000). Thus, similar future studies using the Bentho-torch would be beneficial.

Further, in ecological studies, in order to estimate arthropod population densities pan traps have been shown to be an effective and efficient technique. Several studies have examined pan traps as a sampling technique to collect baseline ecosystem information for arthropod species abundance and diversity, and the potential influence of trap colour on results; however

very few studies have been conducted in the subarctic. Also, as climate change and consequent disturbances such as fire are expected to alter arthropod community diversity and abundance and the timing and source of plant-pollinator interactions, it is vital to gather baseline population information, and to gain further understanding of plant-pollinator interactions, such as floral colour preference. Several studies have found that most insects prefer yellow traps, followed by blue and white; Hoback et al. (1999) found that yellow traps caught approximately 20% more insect families than blue traps, suggesting that in most ecological studies using pan traps to collect insects yellow should mainly be used (Prokopy and Owens, 1983; Hoback et al., 1999). Findings from this study support findings from previous research that most insects prefer yellow pan traps. Furthermore, this study also found that winged insects preferred yellow, and winged insects were the dominant functional group. Importantly, this research showed that pollinator abundance was significantly lower than the other functional groups, and that fire can further decrease pollinator abundance. In arctic and alpine ecosystems the cold and unpredictable weather has typically been thought of as unsuitable for many insect pollinators, resulting in low pollinator diversity, abundance, and activity compared to milder ecosystems, thus identifying keystone plant species to pollinators in these habitats is crucial (Reid, 2011).

Tables

Table 2.1. Summary table of GLMs testing the effect of burned vs unburned sites, spruce vs willow vegetation type, and pan trap colour (yellow, white, blue) on insect abundance by functional groups and total insect abundance. Burned vs unburned sites and vegetation type were modeled as covariates. Statistical significance at $p < 0.05$ is indicated with bold font.

		Winged		**Crawlers**		**Pollinators**		**Total abundance**	
Factor	**df**	x2	**p-value**	x2	**p-value**	x2	**p-value**	x2	**p-value**
Burned/ unburned	1	35.47	**< 0.0001**	32.63	**< 0.0001**	7.21	**0.007**	6.53	**0.011**
Spruce/ willow	1	9.67	**0.002**	3.21	0.073	0.088	0.767	2.85	0.091
Pan trap colour	1	89.22	**< 0.0001**	10.19	**< 0.0001**	3.73	**0.054**	32.64	**< 0.0001**

Table 2.2. MRPP of differences in arthropod community composition/species diversity between burned and unburned sites for all 144 samples (N=144) and 21 arthropod species (N=21). Statistical significance at $p < 0.05$ is indicated with bold font.

	df	**Observed**	**Expected**	**Variance**	**Skewness**	**t-stat**	**A**	**p value**
Sorenson Distances	**1**	0.487	0.498	0.191	-1.456	-8.50	0.024	**< 0.001**

Average within-group distance

Group	**df**	**Euclidean**
1	71	0.451
2	71	0.507

Table 2.3. Summary table of GLMs testing the effect of burned vs unburned sites, vegetation type, and interaction effects of burned vs unburned sites and vegetation type on cyanobacteria, green algae, diatoms, and total concentration of microbes. Burned vs unburned sites and vegetation type (microbes measured on ground or vegetation leaf surface) were modeled as covariates. Vegetation types are spruce and willow. Statistical significance at $p < 0.05$ is indicated with bold font.

		Green algae		**Cyanobacteria**		**Diatoms**		**Total Concentration**	
Factor	**df**	x2	**p-value**	x2	**p-value**	x2	**p-value**	x2	**p-value**
Burned/ unburned	1	7.58	**0.006**	45.31	**< 0.0001**	22.92	**< 0.0001**	26.80	**< 0.0001**
Vegetation/ ground	1	2.13	0.144	24.16	**< 0.0001**	7.47	**0.006**	9.74	**0.002**
Burned/ unburned*vegetation type	1	3.02	0.082	34.89	**< 0.0001**	14.01	**< 0.0001**	15.44	**< 0.0001**

Figures

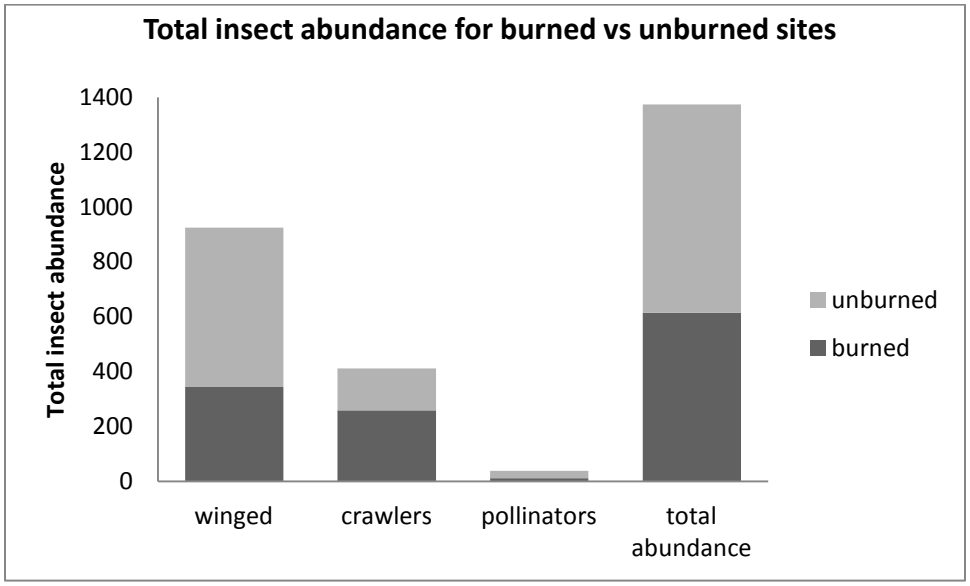

Figure 2.1. Total insect abundance by functional group and total abundance for burned sites (N=47) compared to unburned sites (N=46), all pan trap colours and vegetation types combined (N=282).

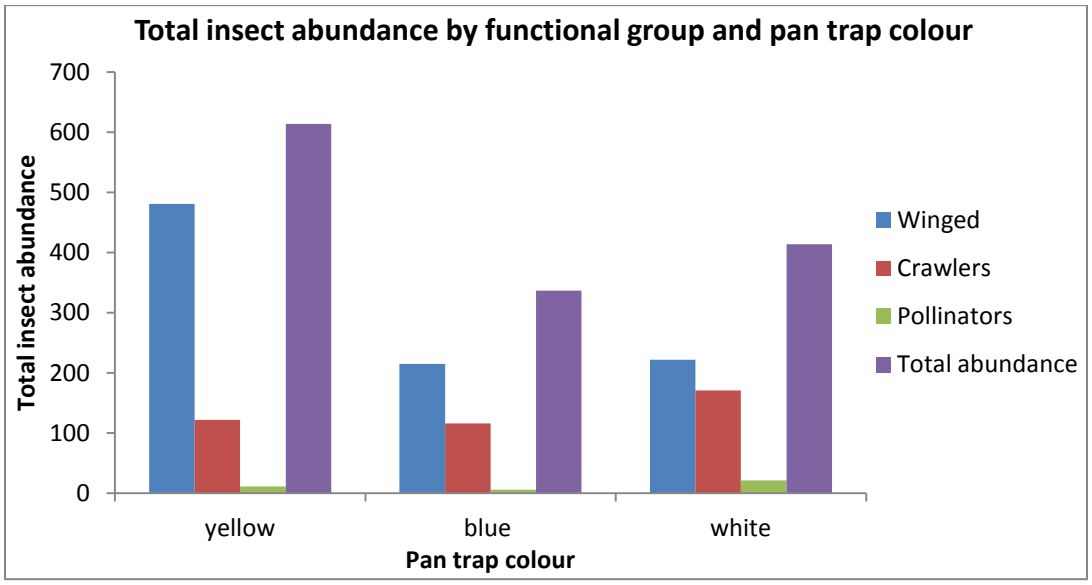

Figure 2.2. Total insect abundance by functional groups and pan trap colour including yellow, blue and white, all sites and pan traps combined (N=282).

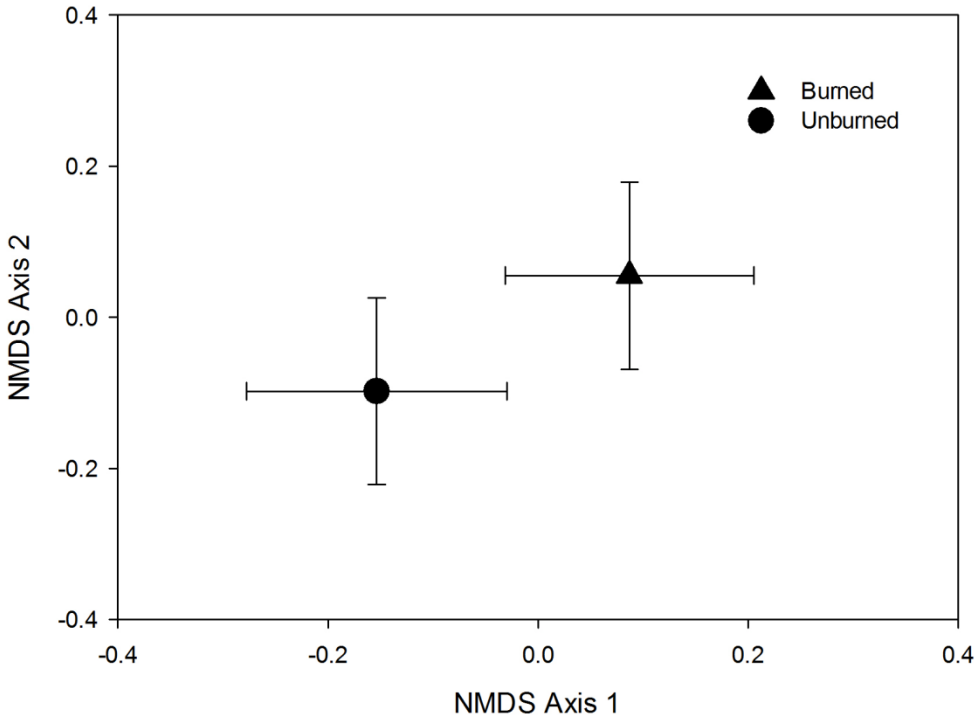

Figure 2.3. NMDS ordination for arthropod species diversity between burned and unburned sites. Error bars plotted are ±1SE for both axes and do not overlap. The groups are significantly different (MRPP $p < 0.0001$).

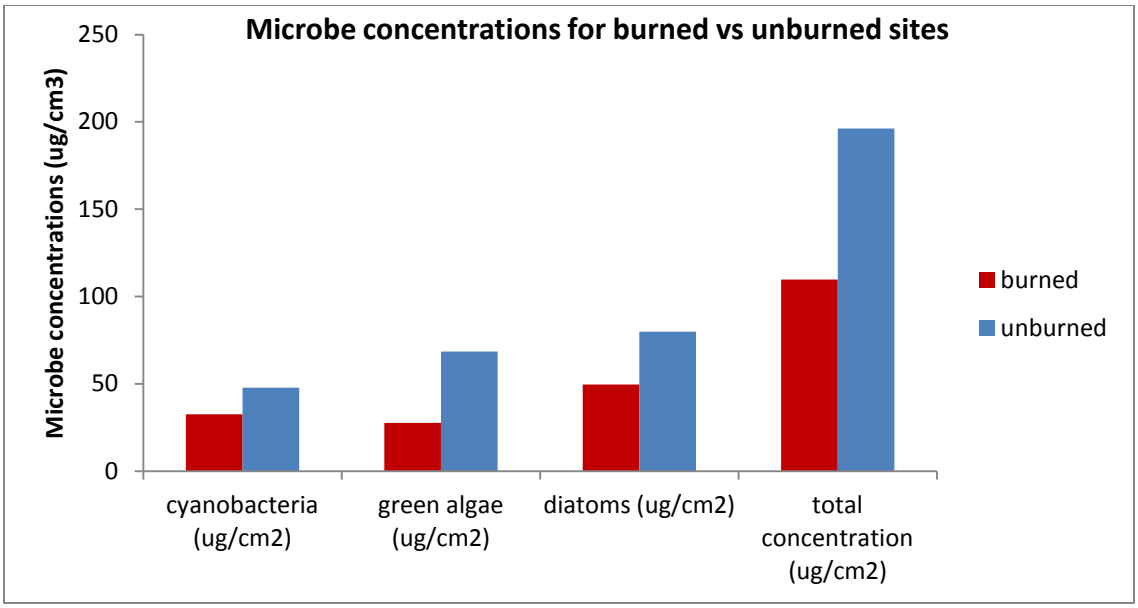

Figure 2.4. Microbe concentrations for burned sites (N=50) compared to unburned sites (N=50) including, cyanobacteria (µg/cm^2), green algae (µg/cm^2), diatoms (µg/cm^2), and total concentration (µg/cm^2), all measurements combined (N=200).

Synthesis of Research

The main objective of this research thesis was to examine how post-fire changes in abiotic and biotic conditions affect the performance and survival of spruce seedlings, and the abundance and diversity of insect and microbe communities in the subarctic of Churchill, Manitoba. Specifically, this research explored the potential impact of fire in changing soil moisture, soil organic layer depth, and shading conditions, as well as plant interactions, as drivers of tree line advancement, and how Boreal ecosystems respond to fire disturbance. This thesis also explored the related topic of how varying colour of pan traps attract distinct groups of insect species, as the pan trap colours mimic flower colours in a pilot study. These research questions collectively help us to better understand the response of species and ecosystems to climate change and the relationship between biodiversity and ecosystem functions for northern ecosystems (Nyakata and McGeoch, 2008; Badano and Marquet, 2008; Shevtsova et al., 1997; Chapin et al., 1995; Eskelin, 2008). Overall, findings from this thesis suggest that fire has significant negative impacts on spruce, arthropod, and microbe communities in a Boreal system. Specifically, post fire changes in soil moisture and shading conditions negatively affect spruce seedling survival and performance, as well as insect and microbe abundance and diversity at the tree line. These findings have important implications as they support the widespread prediction that in response to global warming the tree line will significantly be altered in structure and position, as conifers such as spruce may be replaced by deciduous species, potentially altering trophic interactions further (Danby and Hik, 2001; Brown, 2010; Laliberte and Payette, 2008). Also, findings from studies on impacts of global environmental change on tree line dynamics have detected complex and often contradictory results as the advancement of trees into tundra in recent decades has been widespread but not universal (Harsch et al., 2009; Grau et al., 2012;

Lloyd et al., 2003; Saxe et al., 2001; Hogg and Schwarz, 1997), thus finding from this research add to the growing body of research, suggesting that Canadian tree line forests may not advance northward. A literature review is included in Appendix A, showing that several studies have focused on the effects of fire on tree line dynamics, however few studies have been conducted in Boreal systems, as well as research on spruce performance and survival in relation to the abiotic factors tested is fairly limited.

Also, findings from the pilot study suggest that yellowpan traps are the most effective pan trap colour for capturing insects in a northern ecosystem, as yellow pan traps had the highest arthropod capture rates. Further, spruce seedlings may facilitate winged arthropods, as the type of vegetation that pan traps were placed under only had a significant effect for winged insects, and these insects showed a preference for spruce seedlings compared to willow shrubs. Also, overall, winged arthropods were more prevalent than crawling arthropods, and very few pollinators such as bees were captured. Findings from this research will add to the baseline understanding of plant-insect/microbe interactions in the subarctic, as several studies have focused on plant-plant interactions, including facilitation, however effects of plants on higher trophic levels are rarely examined, and there no studies to date in the Arctic (Liczner and Lortie, 2014; Reid, 2011). Also, current research on trophic facilitation is limited in scope of taxinomical groups studied, typically focussing on aphids, beetles, and mites for example (Reid, 2011). Further, very few studies have used the pan trap method for capturing insects in the subarctic, thus this study shows that pan trapping is a viable technique. A literature review is included in Appendix B. Further the study was unique as it was an extremely dry year where the measured precipitation for the study period was more than 3 standard deviations less than what is normal, which provided the opportunity to research spruce seedling, arthropod, and microbe

responses to post fire changes in abiotic and biotic conditions under extremely stressful conditions, and allowed for control of variability in soil moisture readings, as the soils were relatively dry for the entire study period. These unusual drought conditions also allowed us to show that spruce seedling performance and survival was correlated with soil moisture, demonstrating the negative impacts of moisture stress on spruce trees, and the advantages gained by spruce seedlings located in areas with high soil moisture availability, which relates to tree line dynamics. The Environment Canada climate data is included in a table in Appendix A and B. As the climate warms, moisture stress and fire occurrences in the subarctic will likely become more prevalent, therefore this research provides useful insight into how Boreal tree line ecosystems will respond to climate change. Thus, overall the results from this study suggest that fire and post fire changes in abiotic and biotic conditions negatively impact many trophic levels in a Boreal system at the tree line

In the first study of this thesis, the effects of post fire changes in soil moisture, soil organic layer depth, and shading conditions, as well as plant interactions on spruce seedlings performance and survival were assessed to determine how fire influences tree line dynamics and how Boreal ecosystems respond to fire disturbances in the subarctic of Churchill, Manitoba. The predictions were:

(1) Fire reshapes important biotic factors for spruce seedlings and their survival by reducing soil organic layer depth, soil moisture, and shading, and consequently post-fire abiotic conditions drive tree line dynamics depending on the level of disturbance.

(2) Fire modifies abiotic factors and subsequently the composition of plant species in subarctic ecosystems by inhibiting or promoting the growth and survival of spruce seedlings through competition or facilitation, and plant interactions are a driver of tree line dynamics.

Several spruce performance measures were tested, including spruce seedling height, age, needle density, stem diameter, overall health, and quantum yield. However, a PCA was used to reduce the number of factors, and the results found that age and height were responsible for the majority of the correlated variation and were subsequently used in all additional analyses. Using a Multivariate ANOVA significant differences were found for all abiotic variables between burned and unburned plots, demonstrating that fire changes abiotic conditions, and that fire is the dominant factor in controlling spruce seedlings in a Boreal system at the tree line. Also, using GLMs the results showed that soil moisture and sunlight are important factors for spruce seedling performance. Mean tree density was greatest in burned plots with increased levels of sunlight transmission compared to unburned plots. Also, in burned plots with increased sunlight and soil moisture spruce seedlings were taller compared to unburned plots. Spruce seedlings were also found to be older in all plots with increased soil moisture levels. These findings suggest that as the climate warms and fires become more frequent and severe moisture stress may limit tree line advancement of spruce forests due to the physiological limitations of spruce, and other plant species may outcompete and replace spruce stands. Thus, these results have important implications for forest conservation and restoration management in the Canadian subarctic.

Further, it was also found that the forest which was once dominated by white spruce shifted post-fire to mainly shrub land likely as a result of changes in abiotic conditions and plant interactions. Very little research has been conducted on tree line-shrub dynamics in arctic

ecosystems, and most findings from the existing research (Grau et al., 2012; Chrimes et al., 2005; Maher et al., 2005) show that shrubs have been found to facilitate tree seedlings after fire and/or in harsh environmental conditions, which contradicts findings from this study, where shrubs were found to inhibit the establishment and performance of spruce seedlings as a result of changes in post-fire abiotic conditions, and competition for resources. Thus, in general all of the abiotic factors influenced spruce seedling performance and survival, supporting the widespread prediction that in response to global warming the tree line will significantly be altered in structure and position, as conifers such as spruce may be replaced by deciduous species (Danby and Hik, 2001; Brown, 2010; Laliberte and Payette, 2008). Findings from this research have important implications for tree planting and forest management after fires, as certain species, including spruce may be incapable of post-fire replacement at the tree line as fires become more frequent and severe as a result of climate change, and with resulting increasing stressful abiotic and biotic conditions. Thus, this research demonstrates the importance of understanding how forest communities will respond to disturbances.

Furthermore, the results from several tests were excluded from the thesis as they were not significant, and it was decided that including these results and lengthening the discussion would only reduce the quality of the main body of the thesis for future publication. For instance, the results found that spruce seedlings were taller in all plots with increased organic matter depth; however these results were not included in the thesis because significant interaction effects were found in the model – when there is a significant interaction effect, this implies that the effect of one factor on another is primarily driven by one level, which in this case was burned plots. Further, several tests were conducted on soil samples, such as bulk density, porosity, and loss of ignition, to assess whether these soil characteristic had significant effects on spruce seedling

performance and survival, and whether the soil characteristics were related to soil moisture, soil organic matter depth, or sunlight, however no significant results were found and were thus not included in the thesis.

Furthermore, several studies have found a consistent steep decline in the establishment of conifers on residual organic soils of depths greater than 2.5 cm, while an increase in Boreal tree seedling recruitment, performance, and survival is observed when the burning of surface soil organic material exposed deeper mineral or organic soil layers (Jayen et al., 2006; Jarvis 1966; Chrosciewicz 1974; Clautice 1974; Zasada et al., 1983; Zasada 1985; Weber et al., 1987; Schimmel 1993; Charron and Greene 2002). However, other studies have found negative or neutral effects of burn severity on recruitment (Keays 1987; Schimmel 1993; Sirois 1993; Duchesne and Sirois, 1995). Overall, Johnstone and Chapin (2006) found that negative effects on seedling recruitment occurred beyond a certain threshold of burn severity, where deeply burned soils created moisture stress. Therefore, an ANOVA was also performed to assess whether there was a difference in spruce seedling age and height between organic matter depths grouped into low (<2.5 cm) and high (>2.5 cm). No significant results were found, thus results from this study do not support the hypothesis that a threshold of organic matter depths of 2.5 cm impacts spruce seedling performance or survival.

It was surprising that soil organic matter was not related to spruce seedling performance or survival. A possible explanation is that the burn was not severe enough for soil organic matter depth to play an important role in seedling performance and survival, as the data shows that the majority (approximately 85%) of soil organic matter depths were above 2.5 cm in the burn, and most organic matter depths ranged from 4-8 cm. Other studies found that soil organic matter depth was mostly important for seedlings after fires of intermediate severity, where there was

considerable heterogeneity in soil organic matter depths and deeper mineral soils were exposed, creating optimal conditions for soil moisture stability and availability (Jayen et al., 2006; Jarvis 1966; Chrosciewicz 1974; Clautice 1974; Zasada et al., 1983; Zasada 1985; Weber et al., 1987; Schimmel 1993; Charron and Greene 2002). Also, these studies found that burn severity and soil organic matter depth was more important for seedling recruitment and establishment compared to performance and survival (Jayen et al., 2006; Jarvis 1966; Chrosciewicz 1974; Clautice 1974; Zasada et al., 1983; Zasada 1985; Weber et al., 1987; Schimmel 1993; Charron and Greene 2002), and in this case several of the spruce seedlings were planted. Thus, future studies on the effects of soil organic matter on spruce seedling performance and survival after fire in Boreal ecosystems during more typical weather patterns would be beneficial and would potentially provide an interesting comparison of results for this study.

It was also surprising that that soil moisture was not related to soil organic matter depth. It is possible that soil moisture was independent of soil organic matter because it was a drought year, and when moisture levels are extremely low soil type and characteristics such as water retention or porosity would not play an important role for spruce seedlings – if the soils were relatively dry than there would be a weak or no correlation between soil moisture and soil organic matter. However, the soils were not completely dry, variability in soil moisture was found; thus, it would be expected that soil moisture would be related to soil organic matter, as organic soils have high soil moisture retention capabilities. Shading was also not related to soil moisture, thus it is unclear what factors were responsible for maintaining soil moisture levels. Further, as soil moisture was correlated with spruce seedling performance and survival and it is unclear what factors in this study contributed to soil moisture levels, future studies on factors related to soil moisture availability in Boreal systems might be beneficial, as the implications of

this study suggest that during periods of drought spruce seedlings located in areas with higher moisture availability gain the advantages of increased performance and survival over other spruce seedlings. These findings are important as droughts and moisture stress are predicted to increase with climate warming, and resulting increased fire occurrence and severity, especially in Northern regions where the impacts of climate change are expected to be most pronouced.

The second section of this thesis was a pilot study which explored the capacity for fire in a subarctic ecosystem to influence biotic interactions between spruce seedlings, willow shrubs, arthropods, and microbes by comparing arthropod and microbe abundance between burned and unburned sites. The pilot study also examined the related topic of how varying colour of pan traps (yellow, blue, and white) attract distinct groups of insect species, as the pan trap colours mimic flower colours and research in the subarctic is limited. The main goal of the pilot study was to add to the baseline understanding of plant-insect/microbe interactions in the subarctic and explore the importance of a changing fire regime due to climate change and more generally examine whether these techniques are viable in this ecosystem. The research was considered a pilot study since there was only one sampling period over the course of 24 hours. Thus, similar or replicate future studies would be beneficial, especially as research on plant-insect/microbe interactions in the subarctic is rare, and it was an unusually dry sampling period, which may have affected the results. The predictions were: 1. Arthropod and microbe densities and diversities are higher at sites with willow and spruce present, i.e. unburned vs burned sites. 2. Abiotic drivers such as changes in soil moisture, soil organic matter depth, and sunlight as a result of fire reduce arthropod and microbe abundances and diversities. 3. Total number of plant species is also reduced by fire and thus lower plant species diversity correlates with lower insect and microbe abundance.

Results from this study provided evidence in favour of the hypothesis that fire reduces insect and microbial abundances and diversity in subarctic systems even with the presence of the dominant plant species at those sites. Using a GLM results showed that insect and microbe abundance was significantly greater in unburned sites compared to burned sites, suggesting that fire and post fire changes in abiotic and biotic conditions negatively impact many trophic levels in a Boreal system at the tree line. An NMDS and MRPP ordination analyses also found that the arthropod community composition was significantly different between burned and unburned sites, which also demonstrates that fire impacts insect diversity and can change the community composition of arthropods in the subarctic. These results also supports the hypothesis that dominant plant species such as spruce and willow in Boreal systems facilitate arthropod and microbial communities, as the removal of vegetation cover by fire has been found to play a key role in reducing arthropod abundance, mainly a result of altered habitat conditions, specifically litter biomass, vegetation structure and patterns of ground insulation (York, 2000). Findings from this research have important implications for conservation and restoration management efforts, as arthropod communities comprise the majority of the biodiversity in subarctic ecosystems, and these insect communities may not be capable of adapting to expected increasing fire occurrences and severity as a result of climate warming, especially as many insect groups are sensitive to disturbances. Also, lower trophic levels, including microbes and insects play a vital role in forest ecological processes responsible for the performance and survival of higher trophic levels, and thus this study demonstrates the importance of understanding trophic interactions in response to disturbances, for monitoring the overall health of an ecosystem and for planning purposes.

Further, results for the pan trap pilot study found that yellow pan traps had the highest insect capture rates for all arthropod functional groups and for total insect abundance. Also,

using a PCA it was determined that blue pan trap colour was not a significant factor and was thus removed from all analyses. Overall, winged arthropods were more prevalent than crawling arthropods, and very few pollinators such as bees were captured, which is important as the prevalence of pollinators in northern ecosystems is typically low, and this study suggests that climate warming and resulting fires likely further decreases pollinator populations. Further, the type of vegetation that pan traps were placed under only had a significant effect for winged insects, and these insects showed a preference for spruce seedlings compared to willow shrubs. These results are beneficial for future studies as they suggest that pan trapping is a viable method for studying insect populations in the subarctic. Also, as climate change and consequent disturbances such as fire are expected to alter arthropod community diversity and abundance and the timing and source of plant-pollinator interactions, it is vital to gather baseline population information, and to gain further understanding of plant-pollinator interactions, such as floral colour preference. Specifically, these results suggest that yellow and white pan traps are more effective for capturing insects compared to blue pan traps, and yellow pan traps were most effective out of all of the colours for capturing insects, which somewhat contradicts previous research findings that most insects prefer yellow traps, followed by blue, and then white (Prokopy and Owens, 1983; Hoback et al., 1999). However, as this was only a pilot study with one sampling period, future studies on using pan traps for capturing insects and testing insect colour preference in the subarctic would be beneficial. Therefore, as climate change is expected to be most apparent in arctic ecosystems this study has important implications for the arthropod and microbe communities, especially as the study was conducted during a drought year, providing the opportunity to study arthropod community composition during extreme conditions.

To date, studies on microbes have typically used coarse-resolution DNA fingerprinting methods and phospholipid fatty acid profiles – the BenthoTorch method used in this study is an innovative method, and there is no existing research to date using this technology to study microbe concentrations in three algal classes on northern ecosystems post-fire. Further, plants provide an extremely diverse habitat for microorganisms, and each zone of a plant has its own group of microorganisms with varied relationships (Andrews et al., 2000). Through recent technological breakthroughs, such as the Bentho-torch used in this study, the scientific community is gaining a better perspective of the nature of these relationships, yet still relatively little is known about the role of microbial associations with plants (Andrews et al., 2000). Thus, this study is unique and will add to the literature on microbes, as microbial research in the subarctic is rare and there are currently no studies on plant-microbe interactions in the subarctic. Also, as there was only one sampling period for this study and it was an unusually dry year, future studies utilizing the Bentho-torch method to study microbe populations and microbe-plant interactions in the subarctic over multiple sampling periods and seasons would be beneficial. Further, as the results for this study found that microbe concentrations were significantly higher when measured on the ground compared to vegetative leaf surfaces, it would be interesting for future studies to test microbes not only on the ground surface, but also below the ground, and at different depths. It would also be interesting to experiment with selecting different, or various target plant species for studying both plant-microbe and plant-insect interactions; however, as the results for this study found that microbe concentrations were significantly higher when measured on the ground compared to vegetative leaf surfaces, exploring soil-microbe interactions may be more beneficial.

Overall, this study on plant-insect/microbe interactions in relation to fire at the tree line will make an important and unique contribution to the literature on the response of subarctic ecosystems to climate change, fire, and tree line dynamics, as innovative methods were utilized, including the Bentho-torch for studying microbes, and pan trapping for studying insect populations, which is rare for subarctic research. Also, we had the rare opportunity to study these trophic interactions during an unusual drought year, providing the ability to study how plant, microbe, and insect communities respond to extremely stressful conditions in a natural setting without having to manipulate abiotic factors, allowing valuable insight into how these communities might respond to future climate change and consequent increasing disturbances and stressful conditions.

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Chapter 1

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Appendix A: Chapter 1

Table 1.A1. Environment Canada data for the mean total precipitation (mm) and standard deviation for the month of July 2014, and the 30 year precipitation normal (1981-2010) recorded for Churchill, Manitoba.

Month	**Mean total precipitation (mm)**	**Standard deviation**
July	2.3	6.6
30 year precipitation normal	59.8	N/A

Table 1.A2. ANOVA of differences in age and height (cm) for soil organic matter depths < 2.5 cm and > 2.5 cm for burned plots only, all transects combined. Age is the number of whorls. Statistical significance at $p < 0.05$ is indicated with bold font.

		Sum of Squares	df	Mean Square	F	p value
Age	Between Groups	5.360	1	5.360	.099	.754
	Within Groups	24631.923	453	54.375		
	Total	24637.284	454			
Height (cm)	Between Groups	1134.871	1	1134.871	3.862	.541
	Within Groups	1379687.925	454	3038.96		
	Total	1380822.796	455			

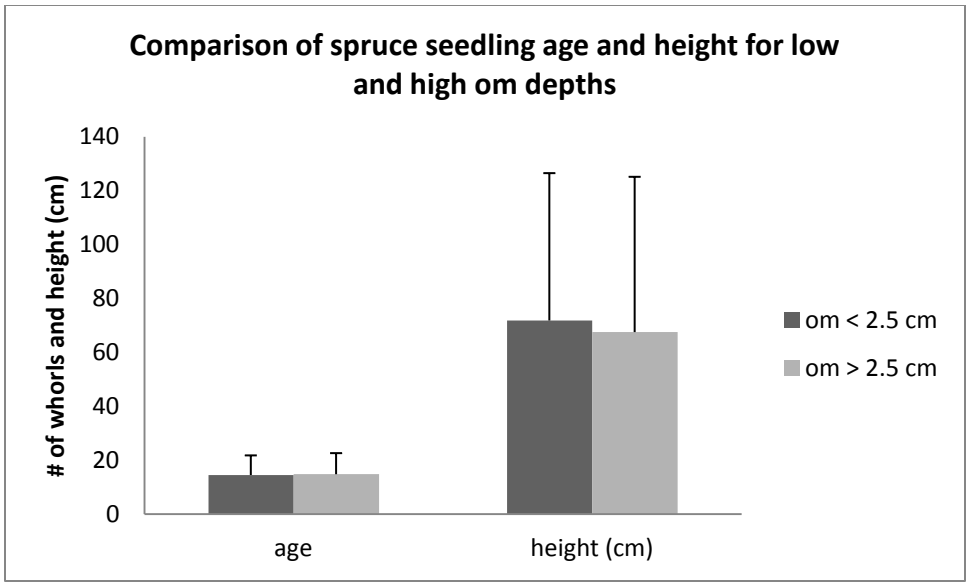

Figure 1.A1. Comparison of spruce seedling age (number of whorls) and height (cm) for soil organic matter depths grouped into < 2.5 cm and > 2.5 cm for burned plots only, all transects combined. Age is represented by the number of whorls.

Table 1.A3. Literature review of the number of results from Web of Science for keywords related to Chapter 1.

Literature Review		
Search Keywords	**Number of Results**	**Database**
Spruce and soil moisture	44	Web of Science
Spruce survival and soil moisture	0	Web of Science
Spruce and soil organic	72	Web of Science
Spruce survival and soil organic	4	Web of Science
Spruce and sunlight	4	Web of Science
Fire and abiotic	12	Web of Science
Spruce survival and sunlight	0	Web of Science
Spruce and shading	25	Web of Science
Spruce survival and shade	1	Web of Science
Spruce and tree line	221	Web of Science
Fire and tree line	118	Web of Science
Fire and tree line and Boreal	35	Web of Science

Appendix B: Chapter 2

Table 2.B1. Multivariate ANOVA comparing soil moisture %, soil organic matter depth (cm), and sunlight % transmission between burned and unburned plots, all transects combined. Statistical significance at $p < 0.05$ is indicated with bold font.

Multivariate Tests

Effect		Value	F	Hypothesis df	Error df	Sig.
Intercept	Pillai's Trace	.806	621.403[b]	3.000	448.000	.000
	Wilks' Lambda	.194	621.403[b]	3.000	448.000	.000
	Hotelling's Trace	4.161	621.403[b]	3.000	448.000	.000
	Roy's Largest Root	4.161	621.403[b]	3.000	448.000	.000
burn	Pillai's Trace	.122	20.835[b]	3.000	448.000	.000
	Wilks' Lambda	.878	20.835[b]	3.000	448.000	.000
	Hotelling's Trace	.140	20.835[b]	3.000	448.000	.000
	Roy's Largest Root	.140	20.835[b]	3.000	448.000	.000

Tests of Between-Subjects Effects

Source	Dependent Variable	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	OM depth (cm)	239.894[a]	1	239.894	34.520	.000
	Soil moisture (%)	736.521[b]	1	736.521	23.399	.000
	Sunlight (%) transmission	.621[c]	1	.621	10.326	.001
Intercept	OM depth (cm)	2934.329	1	2934.329	422.247	.000
	Soil moisture (%)	22808.460	1	22808.460	724.601	.000
	Sunlight (%) transmission	19.388	1	19.388	322.162	.000
burn	OM depth (cm)	239.894	1	239.894	34.520	.000
	Soil moisture (%)	736.521	1	736.521	23.399	.000
	Sunlight (%) transmission	.621	1	.621	10.326	.001
Error	OM depth (cm)	3127.194	450	6.949		
	Soil moisture (%)	14164.766	450	31.477		
	Sunlight (%) transmission	27.081	450	.060		
Total	OM depth (cm)	13783.472	452			
	Soil moisture (%)	118778.820	452			
	Sunlight (%) transmission	199.679	452			
Corrected Total	OM depth (cm)	3367.088	451			
	Soil moisture (%)	14901.287	451			
	Sunlight (%) transmission	27.703	451			

a. R Squared = .071 (Adjusted R Squared = .069)
b. R Squared = .049 (Adjusted R Squared = .047)
c. R Squared = .022 (Adjusted R Squared = .020)

Table 2.B2. Environment Canada data for the mean total precipitation (mm) and standard deviation for the month of July 2014, and the 30 year precipitation normal (1981-2010) recorded for Churchill, Manitoba.

Month	Mean total precipitation (mm)	Standard deviation
July 2014	2.3	6.6
July 30 year normal	59.8	N/A

Table 2.B3. Literature review of the number of results from Web of Science for keywords related to Chapter 2.

Literature Review		
Search Keywords	**Number of Results**	**Database**
Plant insect trophic interactions and Arctic	6	Web of Science
Plant insect interaction and subarctic	4	Web of Science
Plant insect trophic interaction and subarctic	1	Web of Science
Plant microbe interaction and Arctic	32	Web of Science
Plant microbe interaction and subarctic	5	Web of Science
Plant microbe trophic interaction and subarctic	0	Web of Science
Plant microbe trophic interaction and Arctic	0	Web of Science
Microbe and subarctic	34	Web of Science
Microbe and Arctic	248	Web of Science
Microbe fire and Arctic	1	Web of Science
Microbe fire and subarctic	0	Web of Science
Pan trap and Arctic	10	Web of Science
Pan trap and subarctic	2	Web of Science
Pan trap and Boreal	5	Web of Science
Pan trap fire and Arctic	0	Web of Science

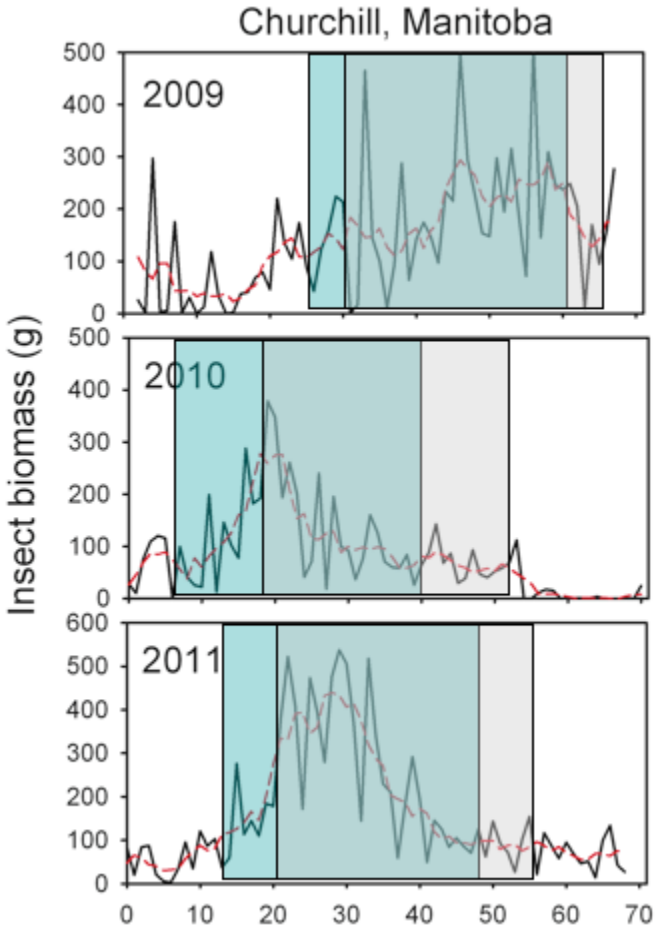

Figure 2.B1. (Senner, 2013). Seasonal peaks in daily insect abundance at Churchill, Manitoba 2009-2011. The black line indicates daily measurements of insect biomass and the red line is a smoothing function subtracting a standard error value for each day. Blue shaded areas indicate the 32 day period of peak mean daily insect abundance each season. Day 1 begins on June 7.

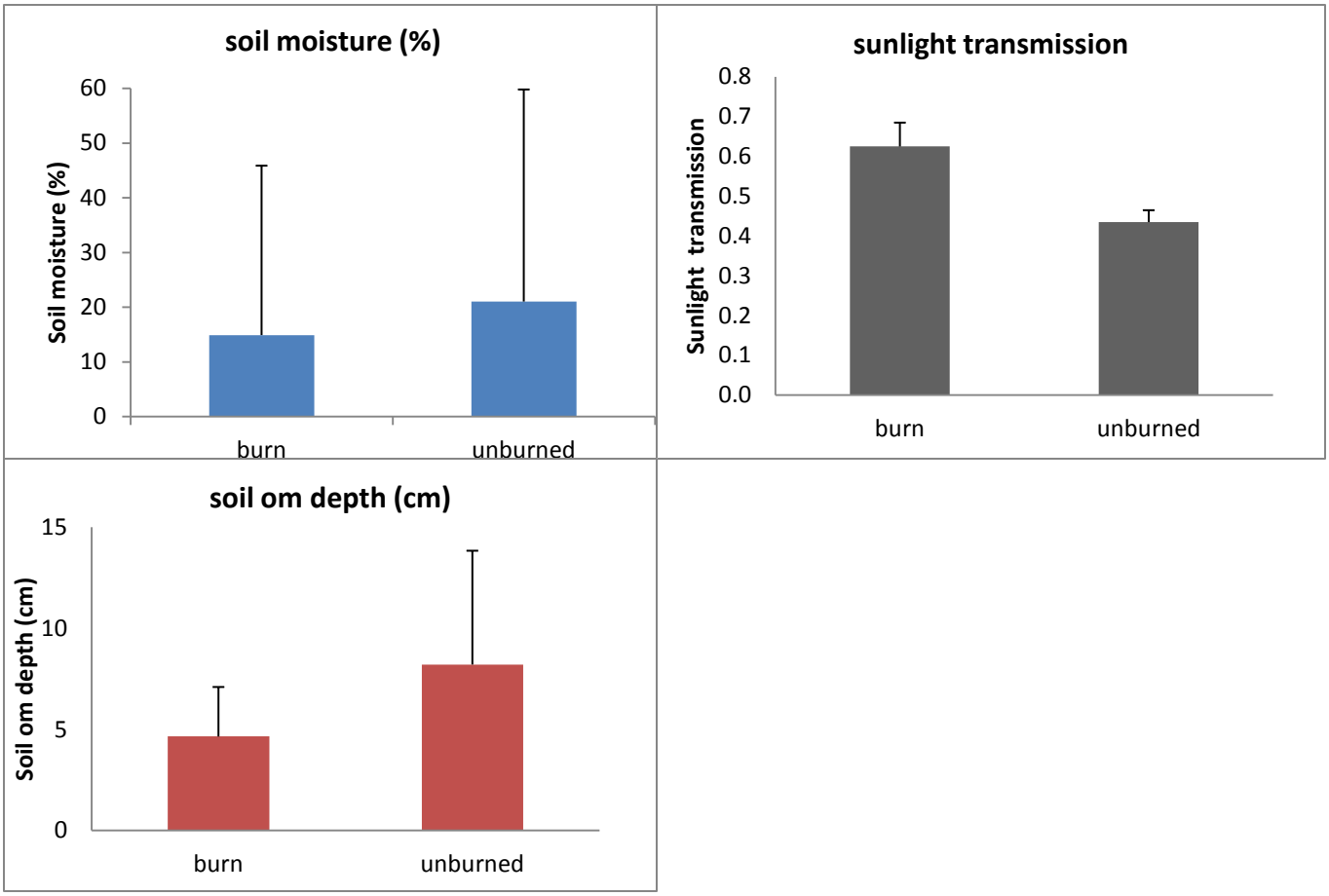

Figure 2.B2. Comparison of average soil moisture % (A), soil organic matter depth (cm) (B), and sunlight transmission (C) between burned and unburned plots using the raw data.